



Calyptraeidae from the northeast Pacific (Gastropoda: Caenogastropoda)

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Abstract

Calyptraeids are sedentary suspension-feeding caenogastropods, which have garnered attention for their protandrous sex change and the propensity of some species to become invasive. The upwelling areas in the northeast Pacific support a particularly diverse calyptraeid fauna, including many poorly known species. This taxonomic review, based primarily on material in the collections of the Natural History Museum of Los Angeles County provides descriptions and photographs of three species of *Calyptraea* Lamarck, 1799, 13 *Crepidula* Lamarck, 1799, three *Crepidatella* Lesson, 1830, and one species each of *Bostrycapulus* Olsson & Harbison, 1953, *Crucibulum* Schumacher, 1817, and *Grandicrepidula* McLean, 1995. Three new species, *Bostrycapulus decorus* n. sp., *Crepidula huertae* n. sp. and *Crepidula wolfae* n. sp. are described.

Key words: *Crepidula*, *Crucibulum*, *Calyptraea*, Slipper snail

Introduction

The Calyptraeidae is a family of distinctive caenogastropods. Colloquially known as slipper snails, cup-and-saucer snails, and hat snails, the conical or patelliform shells of abundant species are widely recognized by biologists and beachcombers. However, numerous poorly known or less common species often co-occur with the iconic ones. With the exception of *Crepidula*, *Bostrycapulus*, and *Crepidatella*, neither the main genera in the family nor the family as a whole have been reviewed since the 1800s. This lack of recent revision combined with variable and plastic shell morphologies means that the identity and relationships of many species are uncertain, even in relatively well-studied regions.

Calyptraeids are particularly diverse along the continental margin of the Eastern Pacific. Areas of upwelling are associated with high calyptraeid abundances (up to hundreds per m²) and species with particularly large body size. Records indicate that a diverse fauna is present along the entire coast, with the highest diversity focused in the Tropical Eastern Pacific with >20 species co-occurring, and diversity dropping to fewer than five co-occurring species in the boreal regions (Hoagland 1977, Keen 1971). This taxonomic review, a tribute to James McLean's contributions to malacology, is based primarily on material in the collections of the Natural History Museum of Los Angeles County and the California Academy of Sciences. The review focuses exclusively on the fauna of the northeast Pacific ranging from northern Baja California to the Aleutian Islands, Alaska. Species with ranges abutting the region covered in this volume, which may incidentally be observed, are *Crepidula excavata* (Broderip, 1834) and *Crepidula incurva* (Broderip, 1834). They are not covered here but information on them can be found in Keen (1958, 1971).

Morphology and biology of calyptraeids. Although calyptraeids have garnered much attention in the literature due to their protandrous sex change, calyptraeid anatomy is dominated by modifications of the ctenidium and mantle cavity for filter feeding. The shell is conical or patelliform and conforms to the substrate. These snails can be found attached to a variety of hard substrates including, rocks, shells, and man-made substrates, especially glass bottles (Fig. 1). All are protandrous hermaphrodites, starting as male and changing to female as they grow (Hoagland 1978, Collin 1995, 2006). Males may be attached to the shells of females in stacks of decreasing size. Early developmental stages are always brooded between the female's

neck, propodium and the substrate (Hoagland 1986), and later development may include planktotrophic larvae, lecithotrophic larvae, direct development from large eggs, oophagy, and adelphophagy (sibling cannibalism) (Collin 2003a). Poecilogony (alternative larval forms) occurs in one species (MacDonald *et al.* 2014). Some species, particularly *Crepidula fornicata* and *Crepidula onyx*, are highly invasive.

Genera are distinguished by overall shell shape, extent of coiling, form and orientation of the internal shelly septum, overall arrangement of internal anatomy, and congruence with monophyletic groups recovered by phylogenetic analyses of DNA sequence data (Broderip 1834, Reeve 1859, Hoagland 1977, Collin 2003a, b, 2005, Collin *et al.* 2007, Véliz *et al.* 2012). Species are usually distinguished by fine differences in shell shape, color, mode of development, and protoconch characters. Shells are plastic, often conforming to the substratum making identification of many species difficult on the basis of shell morphology alone. The distribution of calyptraeids is world-wide with the exception of the polar regions.

Genera in the Northeast Pacific. Six genera are present in the northeast Pacific: *Bostrycapulus*, *Calyptraea*, *Crepidula*, *Crepipatella*, *Crucibulum* and *Grandicrepidula*. Recent revisions of these genera include Hoagland's (1977) review of *Crepidula*, Collin's (2005) review of *Bostrycapulus* and Véliz *et al.* (2012) review of *Crepipatella*. The other genera have not been reviewed since the 1800s (e.g., Broderip 1834, Reeve 1859). All six genera can be clearly distinguished on the basis of shell characters, except that *Grandicrepidula* may be difficult to distinguish from some species of *Crepidula*. The genera also differ in the location and orientation of the major components of the digestive system relative to the mantle cavity. In some cases, this is directly related to differences in shell morphology, but in other cases genera with very similar shells can differ substantially in the anatomical organization (Collin 2003b).

Three genera *Bostrycapulus* Olsson & Harbison, 1953, *Crepidula* Lamarck, 1799, and *Grandicrepidula* McLean, 1995, have roughly similar shell forms. The patelliform shells are humped or convex, they have an oval aperture and the protoconch or shell apex is towards the posterior of the shell. The shells range from bilaterally symmetrical in some species of *Crepidula* to laterally curved or somewhat laterally coiled. Internally there is a broad septum attached laterally along both sides of the shell. *Bostrycapulus* can be distinguished from the others by the shell sculpture, which can include plicate spines, radial ridges and/or nodules, while *Grandicrepidula* is smooth and *Crepidula* species are generally smooth, but can be foliose or take on the ridges of the substrate, but are never spiny or rough like *Bostrycapulus* species. The shape of the anterior edge of the septum, and position of the scars from the shell muscle, which occur on the dorsal shell just anterior to where the septum margin joins the dorsal shell, are also useful features. In *Grandicrepidula* the septum margin extends further forward on right than on the left (all descriptions of the interior of the shell refer to the orientation facing the aperture of the shell with the apex downward, and not the orientation relative to the animal's body) and there is one large muscle scar on the left. In *Bostrycapulus*, the septum has a medial ridge, the margin is sinuate and there is a small muscle scar on the left. In *Crepidula*, the septum margin varies among species and can be sinuate, parabolic or straight but angled forward on the right, and there can be shell muscles on both sides, on the left, or none at all. Anatomically, *Bostrycapulus* is the most distinct of the three genera. In this genus, the mantle cavity does not extend to the distal portion of the visceral mass and the style sac and stomach are visible in the dorsal visceral mass posterior to the mantle cavity. The style sac has a lateral orientation extending from the stomach, which is posterior medial, to the animal's left (Collin 2003b: fig. 3). In *Crepidula* the mantle cavity extends to the distal portion of the visceral mass and the style sac has an anterior-posterior orientation ventral to the mantle cavity. The arrangement in *Grandicrepidula* is somewhat intermediate between the other two genera: the mantle cavity does not extend to the distal portion of the visceral mass, but the style sac is ventral to the mantle cavity (Collin 2003b). The northeast Pacific fauna includes one species each of *Bostrycapulus* and *Grandicrepidula* and at least 13 species of *Crepidula*.

The remaining three genera of northeast Pacific calyptraeids, *Crepipatella* Lesson, 1830, *Calyptraea* Lamarck, 1799, and *Crucibulum* Schumacher, 1817, generally have a circular aperture. Externally, *Crepipatella* is easily distinguishable from the other two genera as the shell apex is posterior (somewhat like *Crepidula*), and internally the septum is distinctly but moderately concave and attached to the shell only along the posterior and left sides. A muscle scar on the left just anterior to the septum is often visible. *Calyptraea* and *Crucibulum* both have conical shells with a roughly central apex. Externally, *Calyptraea* shells are either trochiform and retain some obvious signs of shell coiling or are completely conical, while *Crucibulum* shells retain a slight curve or hook to the shell apex. Internally the septum of *Calyptraea* shells is an inclined plane that traces a loose coil around the shell with the lateral edge attached to the external shell, while the medial edge of the septum either remains free or attaches to near the center of the shell. The septum of *Crucibulum* is

distinctly cup-shaped and attaches to the shell at the center. The septum may be fused to the shell along the left or posterior-left margin in a thin suture, it may be partially open along this side, or it may be closed and almost completely free. The arrangement often changes with size within a species. *Calyptraea* shells are almost always smooth with the exception of the type species *C. chinensis* (Linnaeus, 1758), while *Crucibulum* species generally have some kind of spiny, ridged or rugose shell sculpture. Anatomically, in *Crepidatella* the mantle cavity extends posteriorly to the distal margin of the visceral mass, and the style sac is oriented laterally as in *Bostrycapulus* but is medial to the mantle cavity rather than posterior to it (Collin 2003b). In *Calyptraea* the visceral mass is coiled and the mantle cavity extends to the posterior end of shell but ends well before distal end of the visceral mass. The style sac and stomach are medial to the mantle cavity and the style sac extends posteriorly from the stomach to the posterior shell margin (Collin 2003b). In *Crucibulum*, the stomach and style sac are also medial to the mantle cavity, as in the other two genera. However, the mantle cavity and the style sac both curve posteriorly, counter clockwise around a large plug of connective tissue that fills the cup-shaped septum (Collin 2003b).

Northeast Pacific species. The calyptraeid fauna of the northeast Pacific is fairly well-known, compared to some other gastropod families. However, significant gaps in our knowledge still exist. Of the 22 species reviewed here (see taxonomy below), published DNA sequences from *Bostyapulus decorus* n. sp., *Calyptraea burchi*, *Calyptraea contorta*, *Crepidatella charybdis* and *Crepidula glottidiarum* and true *Crepidula adunca* is lacking. The development of the same six species and of *Grandicrepidula grandis* and *Crepidatella dorsata* has not been described. The anatomy has not been described for these six species and *Crepidatella dorsata*. DNA sequences, including COI, 16S and/or 28S have been published for the remainder of the species (Collin 2003b, c, 2005, Collin *et al.* 2007), as have descriptions of development (Collin 2003a), and a matrix of morphological characters (Collin 2003b).

Another area in need for further research is the taxonomy of the flat white *Crepidula* species, referred to as the “planar group” by Hoagland (1977). Their taxonomy is complicated by the plasticity of the shells and lack of diagnostic shell features. There are a number of species for which DNA sequences and developmental data support distinct status but which do not exhibit diagnostic shell morphology or clearly distinct differences in gross anatomy (see below). Needless to say, the geographical ranges of these species are not currently known with much precision and it is likely that detailed analysis of substrate preferences for each species may help aid field identifications in the future. Finally, the calyptraeids from deeper waters, that are primarily collected by dredging, are poorly known and represented by few (< 20 individuals in some cases) museum samples. Efforts should be made by workers conducting dredging or trawling surveys to preserve as many of these species as possible.

Shell morphology of each species and comments on the soft anatomy when it can be of use in identifying living or preserved material is reviewed below. Most northeast Pacific calyptraeids can be distinguished on the basis of shell morphology, which is the basis of the majority of species descriptions, and the basis upon which species are usually identified in the field by ecologists, conservation practitioners, and by citizen scientists. The mode of development is given, as this is a character easily observed in brooding females and can often be used to distinguish between similar species. Finally, although the soft part morphology of calyptraeids is fairly conservative within a genus, there are some cases where distinctive coloration of the mantle (Figure 1), osphradium morphology, or other aspects of the gross morphology may be of use in identifying living or preserved material. In these cases, the distinctive features are noted.

Abbreviations

CASIZ	California Academy of Sciences, Invertebrate Zoology, San Francisco, California, USA.
CASG	California Academy of Sciences, Geology (fossils), San Francisco, California, USA.
FMNH	Field Museum of Natural History, Chicago, Illinois, USA.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA.
LSL	Linnean Society London, England, United Kingdom.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MNHN	Muséum National d’Histoire Naturelle, Paris, France.
NHMUK	Natural History Museum of the United Kingdom, London, England, United Kingdom.
USNM	United States National Museum, Washington, D.C. USA.

ZIN Zoological Institute, Academy of Sciences, St. Petersburg, Russia.
 OD Original designation.
 M Monotypy.
 SD Subsequent designation.

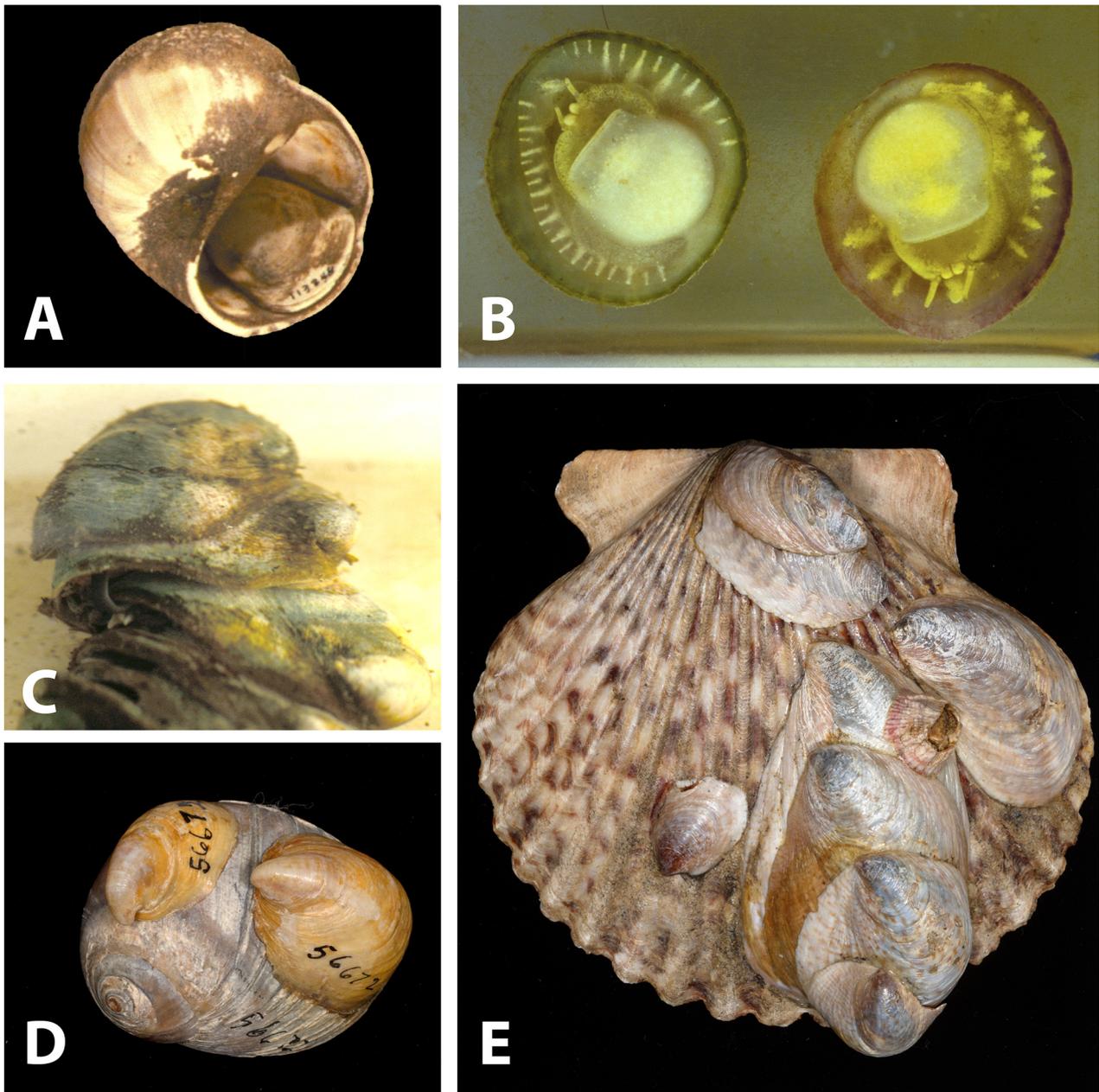


FIGURE 1. Epizootic calyptraeid species in life position. A. *Crepidula plana* in life position inside a naticid shell. B. *Crepipatella lingulata* attached to aquarium wall in Friday Harbor, San Juan County, Washington. These two animals demonstrate the distinctive mantle markings and color variation. C. *Crepidula fornicata* occur in stacks attached to a small rock or a dead shell of a conspecific. D. *Crepidula norrisiarum* is commonly found attached to *Norrisia norrisi* (Sowerby I, 1838). LACM 56672, Del Rey, Monterey County, California, shows specimens attached to *Glossaulax reclusiana* (Deshayes, 1839). E. *Crepidula onyx* occurs on many substrates including gastropod and bivalve shells. LACM 161832, Alamitos Bay, Orange County, California, shows specimens attached to *Argopecten ventricosus* (Sowerby II, 1842).

Systematics

Calyptraeidae Lamarck, 1809

Shell to 80 mm, limpet form, outline round, oval or irregular; nacre absent; septum or shelf formed by extension of columellar border; protoconch and teleoconch usually coiled or curved; sculpture variable smooth or with spines, radial ridges or nodules; periostracum usually thin, occasionally thick, shaggy; operculum absent except in larvae. Head, neck long flattened bearing lateral lappets; tentacles short, eyes at base; mantle cavity deep; ctenidium with long filaments modified for filter feeding, tips of filaments overlying food groove leading along dorsal right side of neck to mouth; anterior mantle margin folded to form food pouch.

Bostrycapulus Olsson & Harbison, 1953

Bostrycapulus Olsson & Harbison, 1953: 279. Type species (OD): *Patella aculeata* Gmelin, 1791: 3693. Holotype ZIN Chemnitz collection 1144.

Description. Shell to 30 mm, oval; Apex coiled, slightly upturned, appressed above shell margin; shelf margin sinuous, slightly less than half the shell length, with medial ridge, shallow notch on right side; muscle scar anterior to shelf margin on left; exterior sculpture spiny.

Remarks. The genus occurs worldwide in the tropics and includes at least nine species (Collin 2005, Collin & Rolàn 2008), which were previously all synonymized as *Crepidula aculeata* or *Bostrycapulus aculeatus*. The genus is easily recognized as it is the only calyptraeid with both a rugose or spiny shell and a posterior shell apex. The species of *Bostrycapulus* are difficult to distinguish unambiguously based on adult shell characters alone, but comparisons of the development and DNA sequence data show they are clearly distinct. When present the protoconch morphology is also helpful.

Bostrycapulus decorus n. sp.

(Figure 2)

Types. Holotype CAS 89574 (Fig. 2 A, B), San Diego Bay, San Diego County, California. Length 11 mm. Paratypes: LACM 3605, intertidal, Cambria, San Luis Obispo County, California. Length 14.5 mm (Fig. 2E). LACM 3606, 2 shells, Point Loma, San Diego County, kelp beds (Fig. 2C). LACM 3607, 2 shells, Army Camp Beach, San Nicolas Island, California Channel Islands, Ventura County, California (Fig. 2D).

Material examined. This species is known only from shells in museum collections. Lots that contain shells with diagnostic protoconchs include:

LACM 19706. Cayucos, San Luis Obispo County. LACM 1974-69.26, 238 m, off Refugio beach, Santa Barbara, Santa Barbara County. LACM 161687. Point Fermin, San Pedro, Los Angeles County, USA. LACM 1956-28.8. Point Loma, San Diego County 30 m. LACM 1972-110.32 12 m, La Jolla, kelp beds, San Diego County. LACM 1972-109.38. 20-23 m, La Jolla kelp beds, San Diego County. LACM 1967-45.55. Todos Santos Island, Baja California. LACM 1971-91.31. 6-12 m. Sacramento Reef, just south of San Geronimo Island, Baja California. CAS 871/1/2. From White Point, San Pedro, Los Angeles County, California. CAS 218285. La Jolla, San Diego County, California. CAS 89574. San Diego Bay, San Diego County, California.

Etymology. The species name *decorus*, a Latin adjective, refers to the beautifully adorned or decorated shell of this species.

Diagnosis. Shell pale, lacking brown markings, open plicate spines from broad radial ribs; Protoconch smooth globose with very fine granulose sculpture separated from second section of protoconch with distinct closely spaced radial ridges and less distinct transverse ridges separated from subsequent teleoconch.

Description. Shell to 25 mm, pale, creamish, with indistinct spiral ridges, evenly spinose with plicate spines; apex postero-lateral, above shell margin, coiled upward. Septum half aperture length, laterally notched on right, central longitudinal fold. Body, unknown; radula, unknown; development, unknown.

Distribution. Cambria, San Luis Obispo County, California, to at least Sacramento Reef, northern Baja California. Intertidal to 20 m. Rare.

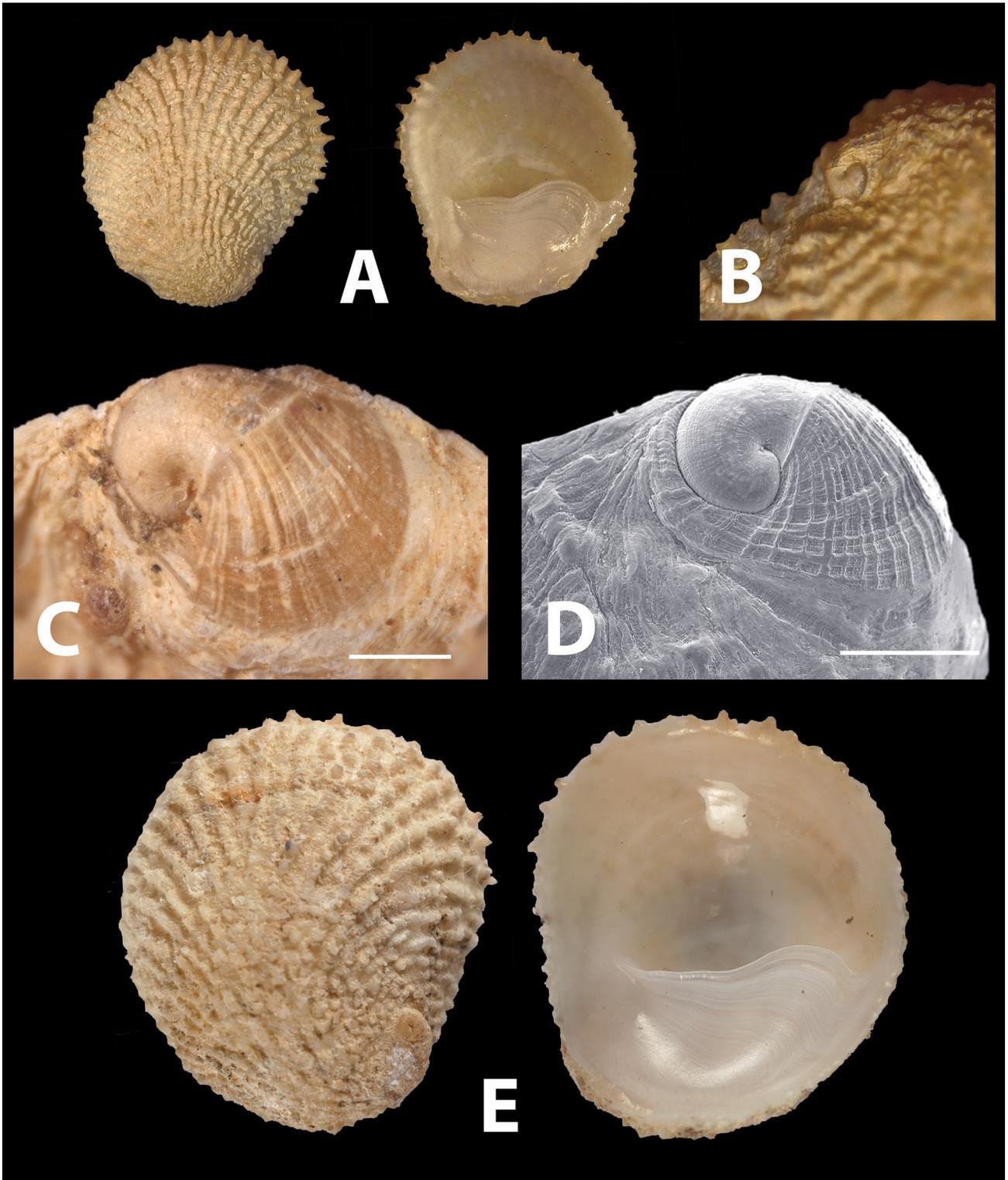


FIGURE 2. *Bostrycapulus decorus* n. sp. A. Holotype shell CAS 089574; San Diego Bay, San Diego County, California. Length 11 mm. B. Holotype protoconch detail. CAS 089574. C. Paratype LACM 3606 protoconch. Point Loma, San Diego County, California. Kelp beds. Sclae bar =500 μ m. D. SEM of protoconch LACM 3607, Army Camp Beach, San Nicolas Island, California Channel Islands, California. Scale bar = 500 μ m. E. Paratype LACM 3605. Intertidal, Cambria, San Luis Obispo County, California. Length 14 mm.

Remarks. This species is smaller and lighter in color than other species of *Bostrycapulus*, which often have brown markings (Collin 2005). The spines occur frequently along radial ridges, which are quite distinct and are not interspersed with smaller ridges that lack spines, as is sometimes the case in other *Bostrycapulus* species. The radial ridges are almost as wide as the spines and the spines rise up like a fold or scale on each, giving them the appearance of ruffles on the ridges. In some shells the radial ridges recede between spines. The protoconchs suggest direct development as they are globose and not particularly coiled. However, it is unusual to see two distinct transitions; one between the smooth globose initial protoconch and the second phase of the protoconch, and the other between this second closely ribbed part of the protoconch and the teleoconch. *Bostrycapulus decorus* is clearly distinct from the geographically closest species, *B. latebrus* Collin, 2005, a species known only from southern Baja California. In *B. latebrus*, there are no striations on the early part of the teleoconch and the same area of the shell is smooth. No museum material examined from Baja California Sur and most material from Baja California Norte either did not retain the protoconch or lacked the ridged sculpture on the protoconch typical of *B. decorus*. The spines on shells from Baja California are not connected by radial ribs, as in *B. decorus*. In the literature (e.g., Hoagland 1977) *Bostrycapulus* from California has been discussed with the *nomen nudum* “*Crepidula californica*”, which was attributed by Tryon (1888) to a Nuttall manuscript, but neither the material nor the manuscript have been found. Live collected shells often have the remains of sponges covering the dorsal surface, suggesting that these animals may be difficult to find in their natural habitat.

***Calyptraea* Lamarck, 1799**

(Figure 3)

Calyptraea Lamarck, 1799: 78. Type species (M): *Patella chinensis* Linnaeus, 1758. Northeast Atlantic.

Galerus Gray, 1847: 157, no. 269. Type species *Patella chinensis* Linnaeus, 1758 (OD). Northeast Atlantic.

Description. Shell to 5 cm, conical or trochiform, usually smooth; shelf attached along lateral margin; columella edge of shelf coiled, central, or not attached; growing edge of shelf often linguiform.

Remarks: The genus *Calyptraea* is in need of revision. In molecular phylogenies, the type species, *C. chinensis*, appears fairly far removed from the other species that have been assigned to the genus; however, this part of the phylogeny is still poorly resolved (Collin 2003b, c). Except for *C. chinensis*, *Calyptraea* species are poorly studied and those from the Northeast Pacific are no exception.

***Calyptraea burchi* Smith & Gordon, 1948**

(Figure 3C)

Calyptraea burchi A. G. Smith & Gordon, 1948: 227, pl. 4, figs 11–13. Holotype CAS 65538. Monterey Bay, California, 20–30 fm.

Description. Shell to 30 mm, low, broadly conical, round aperture, slightly concave sides, chalky white; periostracum thin, tan; apex yellowish-brown; shelf recurved with thick fold on columella side closing at central base, growing edge tongue-like; interior of shell light yellowish-brown, mottled with darker brown flecks. Development, anatomy unknown.

Distribution. Known only from Monterey Bay, California. 30–75 m. Rare.

Remarks. Although significantly larger than *Calyptraea contorta*, the upper half of the shell of the holotype of *C. burchi* is very similar in shape and proportion to shells of *C. contorta*. Material in museum collections is uncommon and DNA sequence data are not available to assess the possible synonymy of these two species at this time.

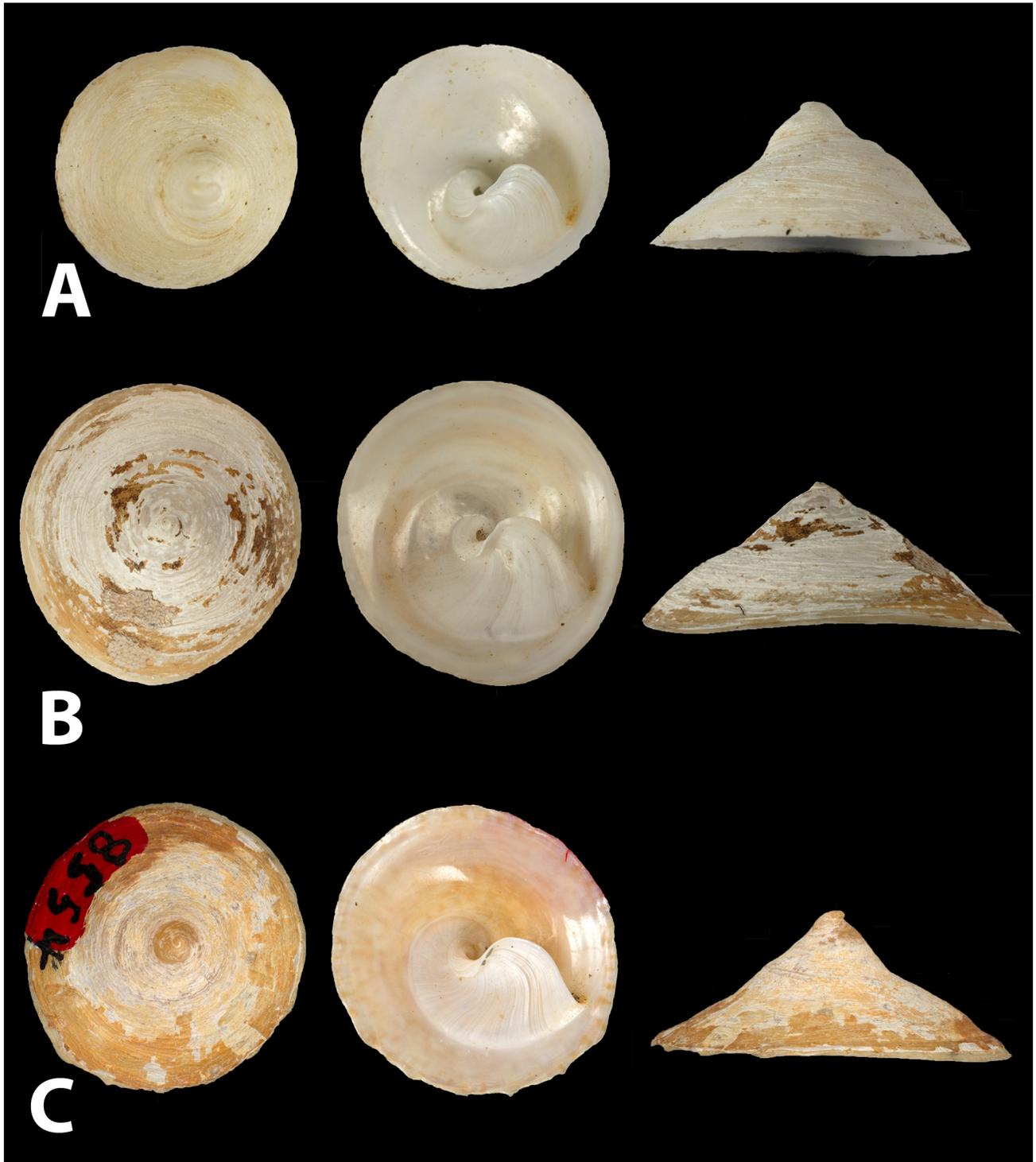


FIGURE 3. *Calyptraea*. A. *Calyptraea contorta* (Carpenter, 1864), LACM 161656, San Pedro, Los Angeles County, California. Diameter 8 mm, height 4 mm. B. *Calyptraea fastigiata* Gould, 1846, LACM 172850, 18 m, Cadboro Bay, Victoria, Vancouver Island, British Columbia, Canada. Diameter 19.8 mm, height 7 mm. C. *Calyptraea burchi* Smith & Gordon, 1948, CAS 065538, holotype, 37–55 m, on shale off Del Monte, Monterey Bay, Monterey County, California. Diameter 16 mm, height 6 mm.

***Calyptraea contorta* (Carpenter, 1864)**

(Figure 3A)

Galerus contortus Carpenter, 1864: 654. Lectotype USNM 11846 (figured in Palmer 1958: pl. 21, figs 13, 14). Santa Catalina Island, California.

Description. Shell to 10 mm, conical, tall, with inflated upper whorls, giving it appearance of irregular top-knot; white, some with remnants of thin tan periostracum; shelf with open fold on columella side, medial edge open coil, growing edge tongue-like. Development direct (R. Collin and B. Pernet unpubl. data). Anatomy unknown.

Distribution. From Monterey County, California and the Farallon Islands to Cedros Island, Baja California. Depth: 30–140 m. Uncommon.

***Calyptraea fastigiata* Gould, 1846**

(Figure 3B)

Calyptraea fastigiata Gould, 1846 [1846–1850]: 161, 1856: pl. 32, fig. 484. Holotype USNM 5874. Puget Sound, Washington.

Description. Shell 5–30 mm, conical, smooth, white, some with thin light brown or tan periostracum; shelf with open fold on columella side, coil of medial edge open, growing edge tongue-like; body white. Development direct. Head, neck, foot, mantle white; Osphradium bipectinate.

Distribution. Anchorage, Alaska, to Puget Sound, Washington. Subtidal to at least 30 m. On rocks. Common.

***Crepidula* Lamarck, 1799**

(Figures 4–6)

Crepidula Lamarck, 1799: 78. Type species (M): *Patella fornicata* Linnaeus, 1758. Elba Island [Italy] (type locality in error). *Ianacus* Mörch, 1852: 146. Type species (OD): *Crepidula unguiformis* Lamarck, 1767. Mediterranean.

Description. Shell to 50 mm, flat to convex or arched, sometimes concave, no sculpture except for growth lines, irregularities from conforming to substrate; shelf attached on both sides, about half aperture length; shelf margin variable; 0–2 muscle scars.

Remarks. *Crepidula* species are diverse in their substrate and habitat preference, which may also modify their shell shape. In general, *Crepidula* species grow to fit their substrate (Fig. 1), meaning that size is often reduced when the animals are attached to small substrates like small snail hosts. Shells can also grow ridges when they occur on ridged substrates like scallop shells. Shells tend to have a lower, flatter profile when they grow on unrestricted flat substrates.

The genus *Crepidula* has been split by some authors based on overall form, with *Garnotia* Gray, 1857, applying to hooked species with two muscle scars, *Grandicrepidula* McLean, 1995, applied to those with a diagonal shelf and *Ianacus* Mörch, 1852, applied to flat white species. However, the available phylogenetic data indicate that these morphologies are convergent in some cases making these groups polyphyletic and in other cases the phylogeny is unresolved (Collin 2003b, c). So there is no support for the monophyly of these groups at this time. Therefore, it is not appropriate to use these genera with the exception of *Grandicrepidula* s.s. (see below). Unfortunately, some of these genus-level names have been introduced into the general biological literature through their use in field guides (e.g., McLean 2007), but their use should be avoided. The white-shelled planar species have been grouped into the polyphyletic *Ianacus*, which is untenable as a genus or subgenus. However, for convenience and ease of comparison, this problematic group of species is treated separately from the remaining *Crepidula* species as the “planar group” following Hoagland (1977). This should not be construed as implying any taxonomic grouping, but is simply to aid comparison amongst this confusing set of species.

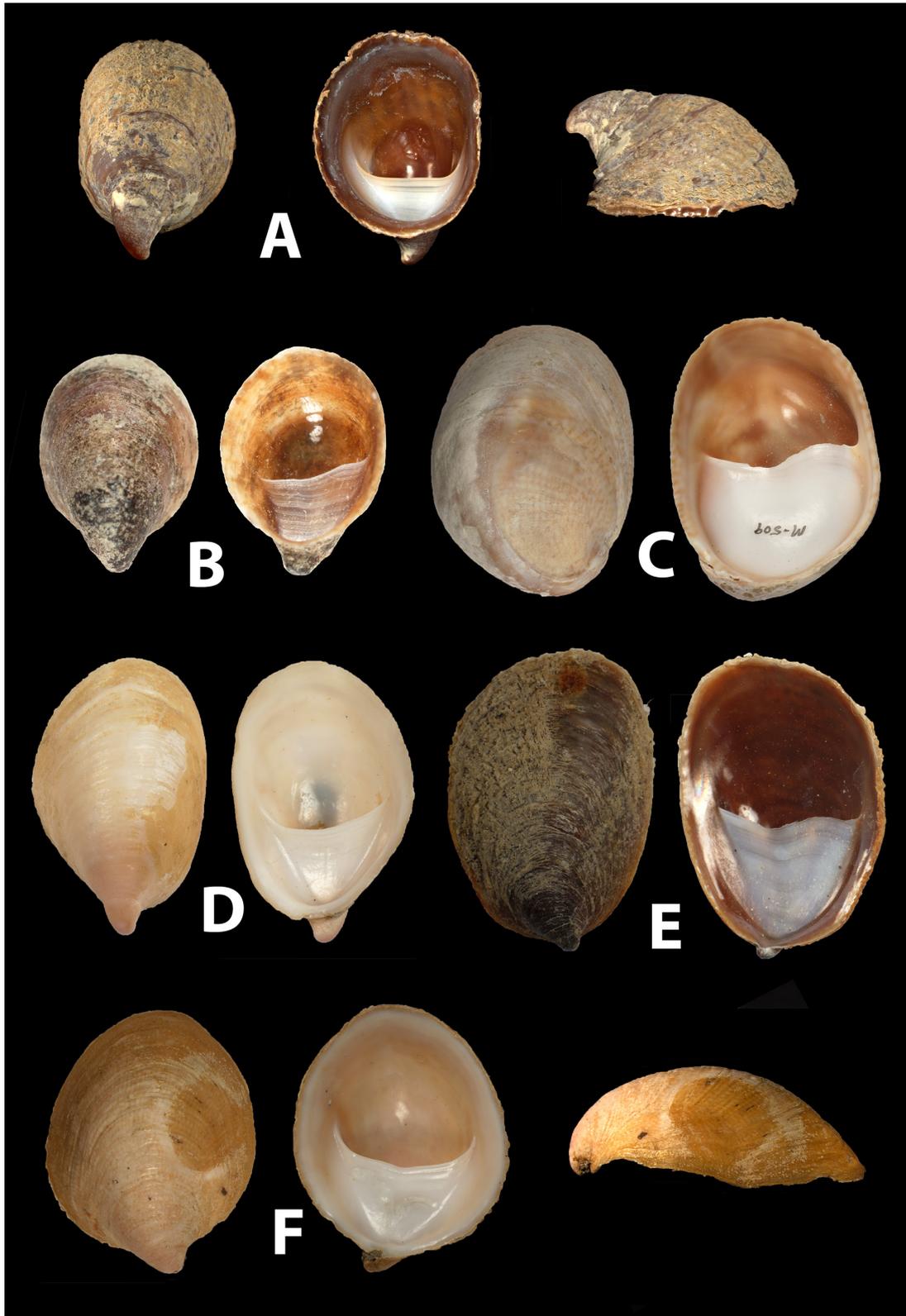


FIGURE 4. *Crepidula*. A. *Crepidula adunca* Sowerby I, 1825. LACM 1942-51.5. Intertidal, North Beach, Cape Arago State Park, Coos County, Oregon. Length 7 mm. B. *Crepidula convexa* Say, 1822. LACM 62-6.5. On *Ilyanassa obsoleta*, San Francisco Bay, Menlo Park, San Mateo County, California. Length 8 mm. C. *Crepidula fornicata* (Linnaeus, 1758). LACM 152861. Intertidal, Oyster Bay, Mason County, Washington Length 35 mm. D. *Crepidula naticarum* Williamson, 1905. Syntype LACM 1026. San Pedro, Los Angeles County, California. Length 20 mm. E. *Crepidula onyx* Sowerby I, 1824. LACM 75-1.11. Intertidal, San Jose lagoon, Guerrero Negro, Baja California. Length 23 mm. F. *Crepidula norrisiarum* Williamson, 1905. LACM 34574. San Pedro, Los Angeles County, California. Length 30 mm.

***Crepidula adunca* Sowerby I, 1825**

(Figure 4A)

Crepidula adunca Sowerby I, 1825 (App.): 7. Holotype NHMUK 1997150. No locality.

Crepidula solida Hinds, 1844: 53, pl. 16, figs 7–8. Type ?. Bodegas, California. 10 fathoms.

Crepidula rostriformis Gould, 1846: 160, 1856, pl. 32, fig. 482. Holotype USNM 5872. Juan de Fuca Strait, Washington.

Description. Shell to 25 mm, small, thin, cap shaped, tan to dark brown, bilaterally symmetrical; aperture oval; apex hooked, above, overhanging posterior margin, internally excavated; septum deeply inserted, white, covering 1/4 of aperture length, extending anteriorly on both sides; muscle scars anterior to septum on both sides.

Distribution. Kachemak Bay, Alaska, definitely to Carmel, Monterey County, California, in museum sample and has been seen live south to Cambria, San Luis Obispo County, California (D. Eernisse pers. com. 2018). Some museum shells suggest possible occurrence to northern Baja California. Intertidal to 20 m. Abundant in northern California to Canada, uncommon in southern California.

Remarks. *Crepidula adunca* occur as epibionts on other gastropods and are particularly common on *Tegula* and *Calliostoma*. There is increasing recognition that *C. adunca* has been consistently confused with the very similar small *C. norrisiarum* in the northern part of *C. norrisiarum*'s range (e.g., Hoagland 1977, Vermeij *et al.* 1987, Collin 2000). Where they occur in sympatry, consistent differences in the morphology of the shell apex (hooked or more appressed) and the extent of excavation of the apex suggest that the small, less hooked and less excavated shells are not *C. adunca* as was previously thought. This would explain the surprising result that the COI sequences reported for *C. adunca* are virtually identical to those obtained from *C. norrisiarum* (Collin 2003c, 2004). DNA sequence data, development and morphology reported for *C. adunca* by Collin (2000, 2003b) is from snails with shells more closely matching the dwarf *C. norrisiarum* morphotype from Friday Harbor Washington, than the hooked and excavated shells matching the type material of *C. adunca*. However additional information on anatomy, development and DNA sequence data is necessary to fully resolve the relationships of *C. adunca* and the large and small morphotypes of *C. norrisiarum*.

***Crepidula convexa* Say, 1822 (introduced)**

(Figure 4B)

Crepidula convexa Say, 1822: 227. Neotype ANSP A19269 (designated by Collin 2002: 178, fig. 1). Cape May, New Jersey.

Crepidula glauca Say, 1822: 226. Neotype ANSP A19269 (designated by Collin 2002: 181, fig. 1). Cape May, New Jersey.

Crepidula acuta H. C. Lea, 1842: 108, pl. 1, fig. 4. Holotype USNM 130473. Delaware Bay.

Description. Shell to 20 mm, convex, oval, tan, brown or purple with darker spots or speckles; apex posterior, near level of margin; shelf extending forward on right side, margin straight or slightly bowed; muscle scar, large, ovate, anterior to septum on left side; development direct. Head, neck, foot and mantle grey; yellowish or cream spots on tentacles. Osphradium monopectinate, leaflets tightly packed.

Distribution. Native to the northeast United States, introduced to the Pacific coast in British Columbia, Washington and California (Collin *et al.* 2006). Intertidal to shallow subtidal. Common where established.

***Crepidula fornicata* (Linnaeus, 1758) (Introduced)**

(Figures 1C, 4C)

Patella fornicata Linnaeus, 1758: 781. Two syntypes LSL 586. Island of Elba, [Italy] (locality in error).

Description. Shell to 50 mm, robust convex, oval, with brown blotches or interrupted, wavy, chestnut-colored markings; apex blunt, turned to right side, merged with margin of shell; shelf flat to slightly concave, half aperture length, margin slightly sinusoidal, slightly notched on right; periostracum absent or thin; muscle scars absent. Development planktotrophic.

Distribution. Native to the east coast of the United States; established in Puget Sound, Washington, and Tomales Bay, and San Francisco Bay, California as well as throughout much of northern Europe. May occasionally occur in central California and Oregon. Intertidal to 60 m. Locally abundant.

***Crepidula naticarum* Williamson, 1905**

(Figure 4D)

Crepidula rugosa naticarum Williamson, 1905: 50. Two syntypes LACM 1026. San Pedro Bay, California.

Crepidula coei Berry, 1950: 36. Holotype CAS 36323.0. Sunset Beach, Orange County, California.

Description. Shell to 30 mm, thin, highly arched, asymmetrical, often steeper pitch on animal's left side; apex tan or pink, remainder of shell tan with mottling or fine radial lines; periostracum thin, tan; apex curved to right, overhanging posterior margin often deeply excavated; septum covers one third of aperture, white, flat, often extending forward slightly on right side, margin straight, without notch; muscle scar large, on left side. Development planktotrophic. Lips, head and neck distinctly asymmetrical, larger on the left side. Osphradium monopectinate, not evenly spaced.

Distribution. From Monterey County, California, to San Diego County and Todos Santos Bay, northern Baja California. Shallow subtidal. On naticid shells inhabited by hermit crabs. Occasionally common.

Remarks. The holotype of *C. coei* is an excellent example of this species. I know of no samples of this species that have been collected from hosts other than hermit crabs inhabiting naticid shells, however little information is available from museum collections.

***Crepidula norrisiarum* Williamson, 1905**

(Figures 1D, 4F)

Crepidula rugosa norrisiarum Williamson, 1905: 50. Four syntypes LACM 1027. San Pedro Bay, California.

Description. Shell to 35 mm, arched, convex, moderately thick, almost bilaterally symmetrical; apex hooked, appressed, curved down towards posterior margin, interior not usually excavated; color light brown under shiny light brown periostracum, often with pinkish apex and interior; shelf white, U-shaped, extending forward on both sides; muscle scars anterior to shelf on each side; development direct. Osphradium monopectinate, sparse, unevenly spaced leaflets.

Distribution. From Puget Sound, Washington, south to at least Punta Banda, Baja California. Subtidal to shallow depths often as an epibiont on the trochid *Norissia norrisi* (Sowerby I, 1838) in California and on smaller trochids further north. Not uncommon.

Remarks. The distinction between *C. norrisiarum* and *C. adunca* needs to be examined in more detail. *Crepidula norrisiarum* living in California on *Norissia* are much larger and appear to be different from those living further north on *Tegula* and *Calliostoma*. However close examination of museum shells show that the significantly smaller northern snails comprise two similar morphotypes, one closely matches typical *C. norrisiarum* from Southern California in everything but size, and the other matches the type material of *C. adunca* (see above). These small animals are similar in morphology, occupy similar habitats, and have all previously been assigned to *C. adunca* (Hoagland 1977, Collin 1995, 2003 a, b, c). DNA sequences recovered by Collin (2003b, c) and anatomical data (Collin 2003a) attributed to *C. adunca* from Washington State, came from these less hooked and less excavated morphotypes. The morphology and DNA sequence results were virtually identical to typical large *C. norrisiarum* from Santa Barbara. This indicates that *C. norrisiarum* is comprised of a large morphotype in the south of its range, which generally occurs on *Norissia* and a dwarf morphotype in the north which occurs on other hosts. No details of the biology of animals with typical hooked and excavated morphologies of *C. adunca* or DNA sequence data have been published. Significant variation in shell shape with size and host occurs throughout the range and it is not always easy to determine if small individuals are *C. adunca* or *C. norrisiarum*.

***Crepidula onyx* Sowerby I, 1824**

(Figures 1E, 4E)

Crepidula onyx Sowerby I, 1824: no. 32, fig. 2. Holotype NHMUK 1977131. No locality.

Calyptraea amygdalus Valenciennes, 1846: pl. 15, fig. 3. Types ?. No locality.

Crepidula rugosa "Nuttall" Carpenter, 1856: 224. 3 syntypes NHMUK 1977156 (Palmer 1958: pl. 14, fig. 6). "Upper California".

Description. Shell to 70 mm, robust, flattish to arched depending on substrate, oval, interior glossy dark brown, exterior brown often with black streak extending forward from apex; apex blunt, turned to right side, merged with margin of shell; shelf white, flat to slightly concave, half aperture length, margin slightly sinusoidal, slightly notched on right; periostracum thick, shaggy; muscle scars absent; development planktotrophic; mantle margin stripped with light, dark pigment; Osphradium monopectinate with tightly spaced leaflets.

Distribution. Southern California, to Baja California, and possibly further south. Introduced in central Puget Sound, Washington, Japan, Korea and Hong Kong. Intertidal to 30 m in bays and lagoons, common elsewhere in low intertidal to shallow subtidal on shells and rocks. Abundant.

Planar Group of *Crepidula*

Crepidula species with flat white shells have evolved multiple times within the genus, occur wherever *Crepidula* are found, and are extremely difficult to tell apart using morphology alone. Other genera of calyptraeids as well as some hipponicids have also converged on this shell morphology. In the northeast Pacific, at least four distinct forms occur: 1) Robust convex shells from snails living on rock surfaces; 2) delicate, elongate, concave shells from snails living within the apertures of gastropod shells occupied by hermit crabs; 3) robust, narrow elongate, shells with foliated edges from snails living in empty pholad holes in rocks; 4) gracile, narrow shells of snails living on the outside shells of *Glottidia* brachiopods. These may represent eco-phenotypic variation within species, or differences among species with very specific habitat preferences or a combination of both. In my experience collecting along the coast of Washington and California each morphotype found in the same region had sufficient genetic and developmental differences to consider them to be distinct species. Similarly, the same morphotype found in different ends of the region also often had sufficient genetic and developmental differences to consider them to be distinct species. In general, these species are under-studied and additional research may help clarify the distributions, habitats and morphospace occupied by each species. The treatment here follows the names that were linked to DNA sequence and developmental data in Collin (2003b, c, 2004). The east coast *Crepidula plana* Say, 1822, (Fig. 1A) has been reported as introduced into San Francisco Bay (Carlton 1992). As a number of native species cannot be distinguished from *C. plana* on the basis of shell morphology or overall appearance of the animal, this occurrence should be treated as provisional until DNA sequences are available. *Crepidula plana* is a well-known species in New England and is not discussed further here.

Crepidula fimbriata Reeve, 1859

(Figure 5A)

Crepidula fimbriata Reeve, 1859: pl. 2, fig. 11. Three syntypes NHMUK 1977132. Vancouver Strait.

Description. Shell to 30 mm, robust, somewhat convex, often with rough surface, occasionally with foliations or lamina around the margins, overall white, with a dark brown stain or smear often visible inside; shelf margin slightly sinuous with lateral notch; muscle scars absent. Development direct.

Description. Jakalof Bay, Kenai-Cook Inlet, Kenai Peninsula Borough, Alaska, to Friday Harbor, San Juan County, Washington. Subtidal, under rocks to at least 20 meters. Uncommon.

Remarks. The species description includes a clear reference to a shell "...of pure white substance, marked on one side with a single dark ray...". This feature can be used to distinguish *C. fimbriata* from similar white species. In Friday Harbor, Washington, this species is found in rock-rubble and often co-occurs with *Crepidatella lingulata*.

Crepidula glottidiarum Dall, 1905

(Figure 5B)

Crepidula nivea cf. *glottidiarum* Dall 1905: 26 Lectotype USNM 183455 (McLean 1996: 52). San Pedro, California.

Descripton. Shell to 25 mm, delicate, elongate, oblong, bilaterally symmetrical, white; apex at posterior margin; shelf covers 1/2 aperture length, margin straight, extending anterior on each side; muscle scars absent; Periostracum tan, smooth. Development unknown. Anatomy unknown.

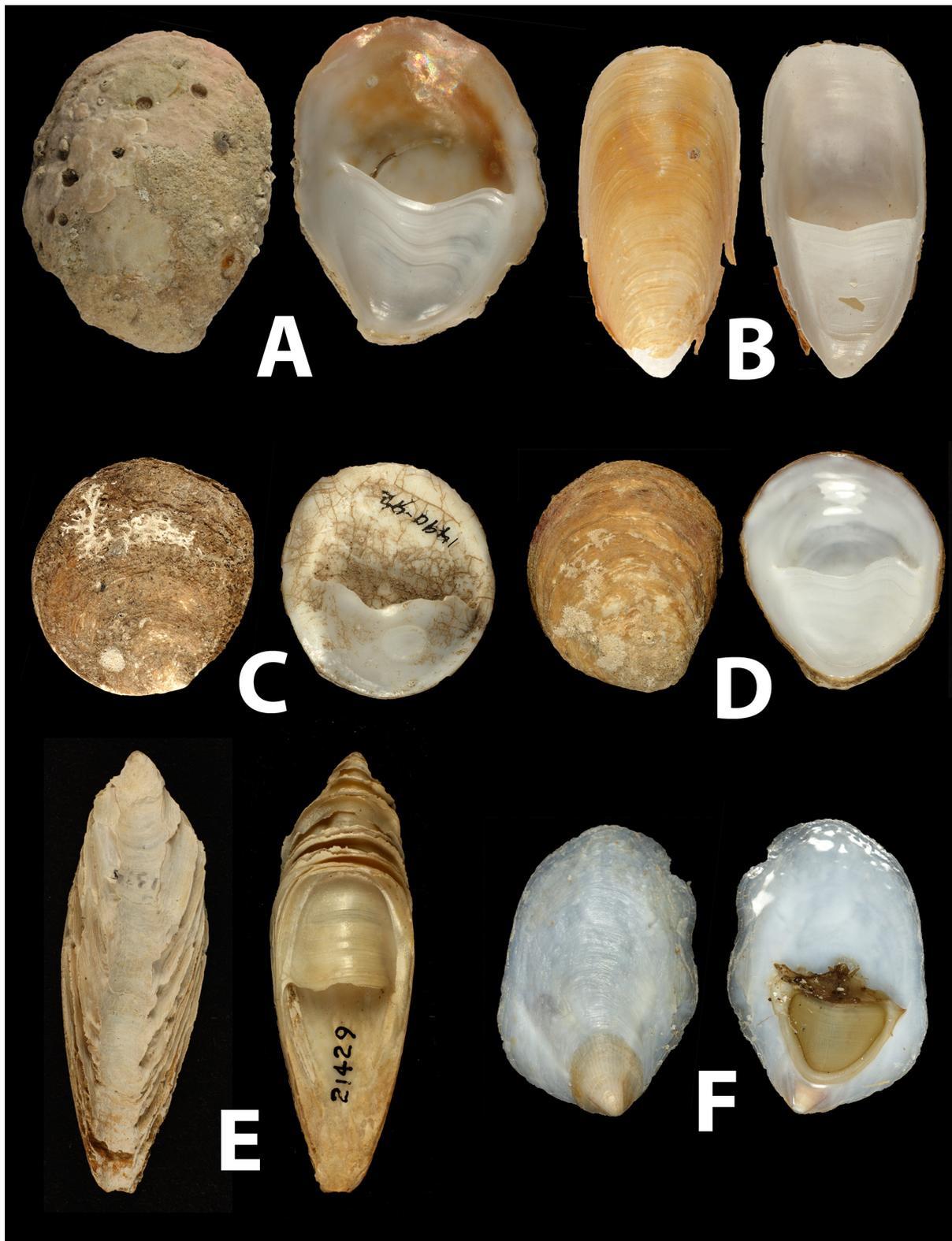


FIGURE 5. Planar Group *Crepidula*. A. *Crepidula fimbriata* Reeve, 1859. LACM 1986-286.15, 2 m, Seldovia Point, S. side Kachemak Bay, Kenai-Cook Inlet County, Alaska. Length 25 mm. B. *Crepidula glottidiarum* Dall, 1905. LACM 1957-134.5, 50 m, off San Clemente, Orange County, California. Length 13 mm. C. *Crepidula nummaria* Gould, 1846. Typical morphotype. LACM 1948-48.21. Cape Argo lighthouse. Coos County, Oregon. Length 31 mm. D. *Crepidula nummaria* Gould, 1846. Unconstrained morphotype. LACM 1963-1.40 Intertidal, Moss Beach, San Mateo County, California. Length 39 mm. E. *Crepidula perforans*, Valenciennes, 1846. LACM 161819, 37 m, off San Pedro, Los Angeles County, California. Length 37 mm. F. *Crepidula williamsi* Coe, 1947. LACM 71-90.32, 9-12 m, San Martin Island, outer coast of Baja California. Length 20 mm.

Distribution. From Point Conception, Santa Barbara County to Laguna Beach, Orange County, California. 20–70m, on the valves of *Glottidia albida* (Hinds, 1844). Rare.

***Crepidula nummaria* Gould, 1846**

(Figure 5D)

Crepidula nummaria Gould, 1846: 160; 1852: pl. 32, fig. 480. Holotype USNM 5870. Classet, Straits of Fuca, Washington.

Description. Shell to 40 mm, flat, round, robust; shelf often convex extending out ventrally past margin of shell; apex usually eroded; periostracum thick, dark, shaggy. Anatomy unknown.

Distribution. British Columbia, Canada, to San Luis Obispo County, California. Intertidal and shallow subtidal. Uncommon but abundant in some museum collections.

Remarks. Shells with the diagnostic thick dark periostracum are typically very flat and round, but some have an oval shape, more typical of other *Crepidula* species. One can imagine that these animals grow in a very particular evenly concave habitat, possibly depressions made by sea urchins. However no observations of their ecology have been published despite some rather large numbers of shells in various museum collections. Development was reported to be direct for this species (Dehnel 1955), however this should be confirmed as the taxonomic confusion among the planar group species brings into question reports that do not describe the adult snails in detail or deposit vouchers.

***Crepidula perforans* Valenciennes, 1846**

(Figure 5E)

Crepidula perforans Valenciennes 1846: pl. 24, fig. 9. Type is lost. Pacific America.

Crepidula explanata Gould, 1853: 377, pl. 14, fig. 7. Holotype MCZ 169137. Monterey, California.

Crepidula exuviata “Nuttall,” Reeve, 1859: pl. 5, fig. 28. Three syntypes NHMUK 1977138. Monterey, California.

Description. Shell to 40 mm, white, elongate, laterally convex, foliated; shelf margin slightly sinuous with lateral right notch; muscle scars absent; shelf often convex, extending out ventrally past margin of shell.

Distribution. Van Damme State Park, Mendocino County, to Palos Verdes Peninsula and San Pedro, Los Angeles County, California. Depth range is poorly documented, but this species seems to be limited to shallow water. Common in collections; patchily distributed.

Remarks. The type for this species is a morphotype from a pholad hole. It is unclear if all individuals conform to such a morphology or if this species inhabits a number of shelters, which could impart different morphologies on the shells. Nevertheless, the distinct pholad morphology is linked to the name *C. perforans*. The single sequenced individual, FMNH 299407, collected from a pholad hole in Santa Cruz and matching this species description had a COI sequence that was >5% divergent from any other *Crepidula* that has been sequenced (Collin 2003b, c).

***Crepidula huertae* n. sp.**

(Figure 6A)

Crepidula cf. *perforans* sensu Collin 2003a, b, c, 2004.

Holotype. FMNH 282243. Naples Reef, near Santa Barbara, California. Live collected from shell inhabited by a hermit crab. Length 30.4 mm.

Etymology. The species name *huertae* is an honorific for Dolores Clara Fernández Huerta in recognition of her activism in support of social justice and the environment in California.

Diagnosis. Shell thin, white, smooth, flat or concave; protoconch white; body white; development planktotrophic; larvae with single black spot at base of velum, several (<10) large yellow spots around velum margin, black pigment in food groove.

Description. Shell to 40 mm, thin, white, smooth concave; shelf convex; muscle scars absent, typical morphology of *Crepidula* from inside gastropod shells inhabited by hermit crabs. Development planktotrophic; egg size 135 microns; hatchlings 239 microns (Collin 2003); body white; osphradium monopectinate.

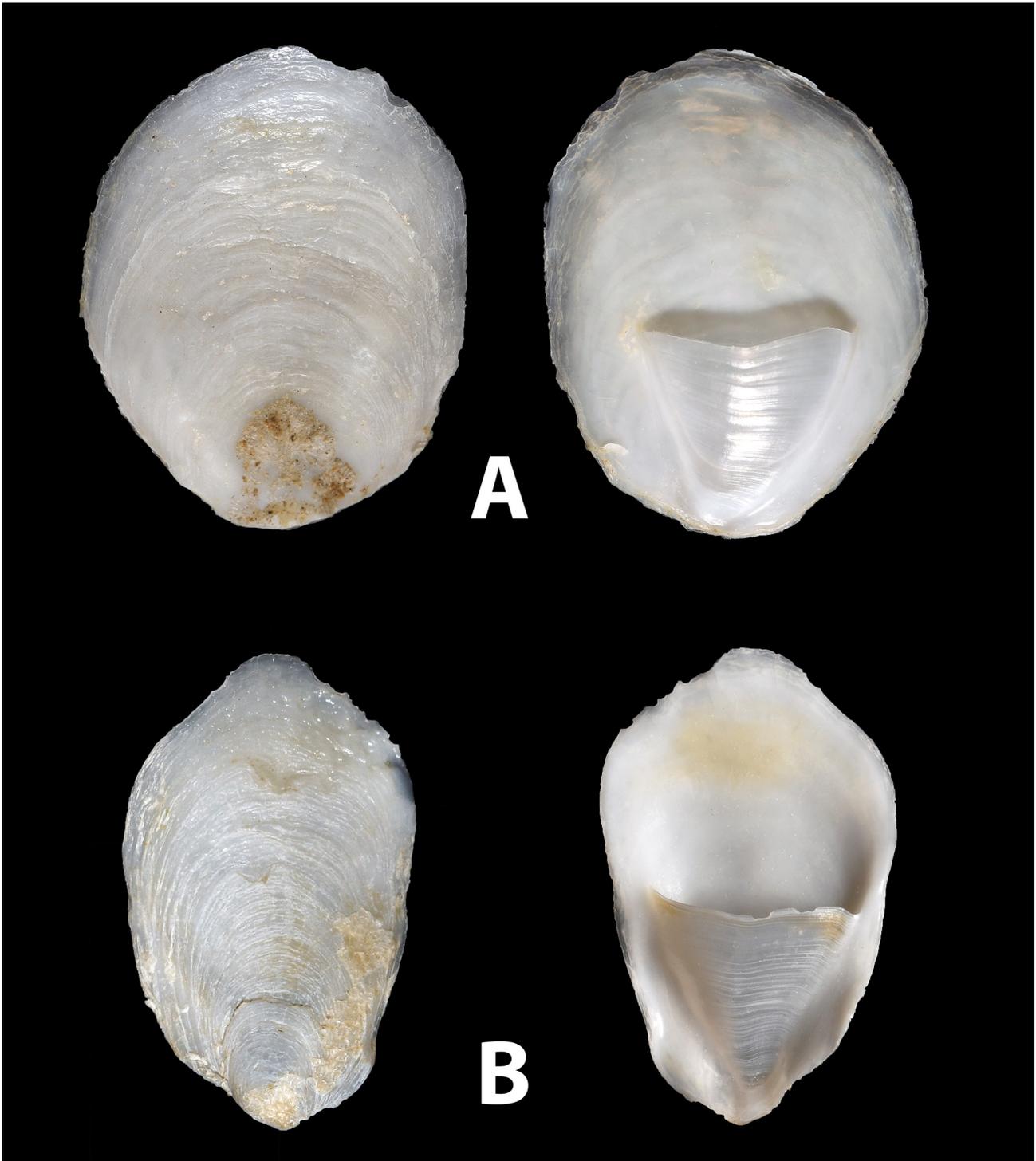


FIGURE 6. Planar Group holotypes. A. *Crepidula huertae* n. sp. FMNH 282243. Subtidal in hermit crabbed shells, from Naples Reef, near Santa Barbara, Santa Barbara County, California. Length 30 mm. B. *Crepidula wolfae* n. sp. FMNH 287485. Miller Point, Fort Abercrombie State Historic Park, Kodiak Island, Kodiak Island County, Alaska. Length 17 mm.

Distribution. Definitive material collected only from Santa Barbara, California. Subtidal, 5–20 meters. Possibly common in shells occupied by hermit crabs.

Remarks. This species was previously referred to as *C. cf. perforans*. Molecular phylogenetic analysis showed that *C. huertae* is distinct from the single sequence available from *C. perforans* collected from a pholad hole in Santa Cruz, California (FMNH 299407). In fact, *C. huertae* falls into a separate clade of flat

white *Crepidula*, which includes the flat white species from the east coast of the United States. The >10% divergence in COI of this species from any other species of *Crepidula* sequenced so far, as well as its being the only flat white species from the northeast Pacific with planktotrophic development, and the distinctive larval pigmentation give ample support for the distinct species status of *C. huertae*, despite the lack of diagnostic shell characters.

***Crepidula williamsi* Coe, 1947**

(Figure 5F)

Crepidula williamsi Coe 1947: 241 fig. 6. Holotype CAS 064338. Coronado Islands, Baja California, 16 m.

Description. Shell to 40 mm, thin, flat, white, smooth, typical morphology of *Crepidula* from inside gastropod shells inhabited by hermit crabs; apex with fine brown radiating lines abruptly ending slightly past protoconch-teleoconch boundary; shelf margin slightly sinuous with lateral notch; muscle scars absent. Development direct. Embryos with yolk in head vesicle.

Distribution. From Santa Barbara, California, to San Martin Island, Baja California. Intertidal to at least 30 meters in shells occupied by hermit crabs. Uncommon.

Remarks. The characteristic brown markings on the early shell can vary in extent and are often missing if the protoconch is eroded.

***Crepidula wolfae* n. sp.**

(Figure 6B)

Crepidula aff. *williamsi* sensu Collin 2003b, c, 2004.

Holotype. FMNH 287485. Miller Point, Fort Abercrombie State Historic Park, Kodiak Island, Alaska. Length 17.0 mm.

Paratypes. FMNH 344599 Miller Point, Fort Abercrombie State Historic Park, Kodiak Island, Alaska. 26 individuals in ethanol.

Other material: FMNH 299429. Shady Cove, Friday Harbor, San Juan Island, Washington (1 animal).

Etymology. Named for Hazel Wolf for her environmental and social activism and her work to forge alliances between conservationists and indigenous communities in Washington State.

Description. Shell to 40 mm, thin, flat, white, smooth, typical morphology of *Crepidula* from inside gastropod shells inhabited by hermit crabs; septum margin slightly sinuous, lateral notch present or absent; muscle scars absent. Protoconch, early shell white or brown; development direct; embryos with flat coiled shell, yolk in head vesicle during middle of development, no obvious velum.

Distribution. Kenai-Cook Inlet, Alaska, to Friday Harbor, Washington. Subtidal to at least 30 m. Uncommon.

Remarks. The name *C. aff. williamsi* was previously applied to this species as molecular phylogenetic analyses place this as the close sister species to *C. williamsi*. This species is genetically distinct, but there is only 3% divergence in COI sequences between *C. wolfae* and *C. williamsi* (Collin 2003b, c, 2004). However the ranges are significantly disjunct with *C. wolfae* not being reported south of Puget Sound so far and with *C. williamsi* ranging from Baja California, as far north as Santa Barbara, California. The early shell of *C. wolfae* lacks the distinctive stripes that are often present on *C. williamsi*, although the early shell can be brown. Unfortunately too few shells are available to fully assess the extent of variation in this feature. Overall for *C. wolfae*, the life habit and adult shell morphology, typical of species inhabiting hermit crabbed shells, is very similar to *C. williamsi*. The direct development is also similar to the development of *C. williamsi*, both have embryos with yolk extending into the transparent head vesicle during mid-development, an unusual feature for *Crepidula* embryos. At ~12°C development took three months when capsules were raised in a dish away from their mother. This species was referred to as *C. explanata* in Collin (2003a) but additional study has shown this not to be correct.

***Crepipatella* Lesson, 1830**
(Figure 7)

Crepipatella Lesson, 1830: 389. Type species (OD): *Calyptraea (Crepipatella) adolphi* Lesson, 1830 [= *Crepidula peruviana* Lamarck, 1822]. Chile.

Verticumbo† Berry, 1940: 8. Type species (OD): *Verticumbo charybdis* Berry, 1940. California.

Description. Shell broadly oval or round, inflated, convex, curved only near apex; apex near posterior margin; septum concave, attached to shell at left side, posteriorly, with deep notch or sinus on right side. Single muscle scar on left at edge of septum. Stomach, style sac lateral to mantle cavity.

Remarks. *Crepipatella* species are particularly abundant and diverse in South America. In the northeast Pacific only *C. lingulata* is commonly encountered. The tropical and subtropical *C. dorsata* is small and cryptic making it difficult to find in the field; *C. charybdis* occurs primarily in deep water.

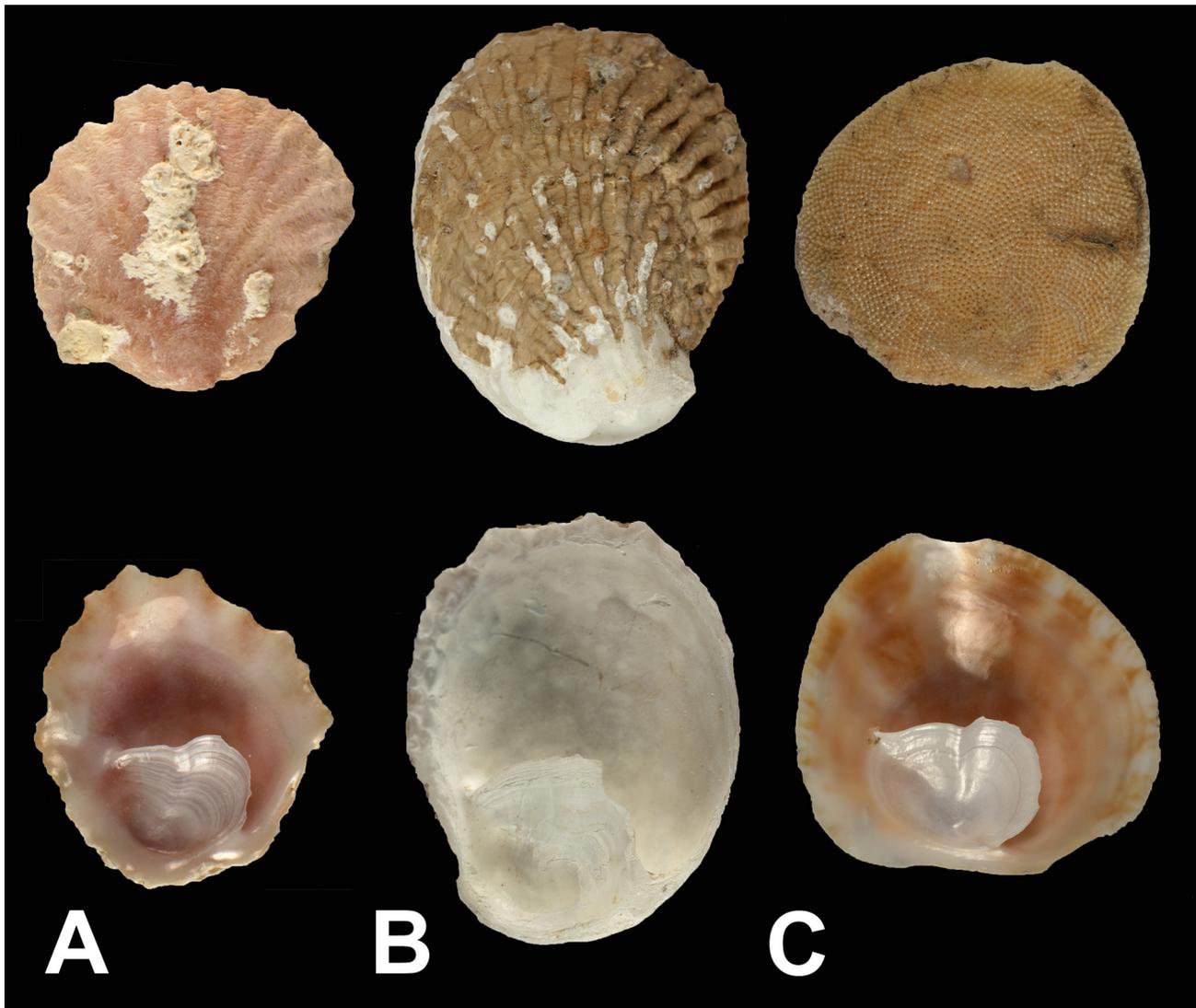


FIGURE 7. *Crepipatella*. A. *Crepipatella dorsata* (Broderip, 1834). LACM 1971-93.30, 12–15 m, off SW tip Cedros Island, Baja California. Length 11 mm. B. *Crepipatella charybdis* (Berry, 1940). LACM 64-109.11, 2,086 m, Cascadia Abyssal Plain off Oregon. Length 15 mm. C. *Crepipatella lingulata* (Gould, 1846). LACM 1960-23.30, 37 m, Hopkins marine station, Pacific Grove, Monterey Bay, Monterey County, California. Length 19 mm.

***Crepidatella charybdis* (Berry, 1940)**

(Figure 7B)

Verticumbo charybdis Berry, 1940: 8, pl. 1, figs 6–10. Holotype CASG 71878. Lomita Formation, San Pedro, California. Paratypes SBMNH 34506.

Description. Shell to 26 mm, round to oval, smooth or with sculpture of weak to strong widely spaced, thick, rounded, occasionally divaricate bifurcating ribs; apex close to posterior margin; early teleoconch with fine spiral sculpture to diameter of 1.3 mm; sculpture coarse emerging at later growth stage when present; shelf concave, attached on left side, posteriorly, free along right side. Development unknown, protoconch large, indicating direct development.

Distribution. Cascadia Abyssal Plain, Oregon, to Santa Cruz Island, California. 150–2,086 m. Extremely rare.

Remarks. This species was described from a Pleistocene fossil but was recognized as a living deep-water species by McLean (1996). Berry (1940) noted both sculptured and smooth forms in the Pleistocene species he described as *Verticumbo charybdis*. The holotype has ribs. Additional study may lead to further clarification of the identity of the modern and fossil species. The deep-water habitat is unusual for calyptraeids.

***Crepidatella dorsata* (Broderip, 1834)**

(Figure 7A)

Calyptraea dorsata Broderip, 1834: 38; 1835, pl. 28, fig. 10. Syntypes NHMUK 1977099. Santa Elena, Ecuador.

Description. Shell to 15 mm but usually much smaller, irregular in outline, with radial sculpture of irregular ridges, forming digitations at margin; septum concave, attached on left side, posteriorly, free along right side; apex often indistinct; shell color white to pink or lavender; development unknown.

Distribution. Cedros Island, Baja California, to Ecuador. Intertidal to 15 m. Rare.

Remarks. The species is sympatric with the larger-shelled *C. lingulata* in the northern Mexico. They are easily distinguished as *C. lingulata* is usually smooth with an even margin, unless it is conforming to the substrate, while *C. dorsata* is ridged and irregular around the edges regardless of the substrate.

***Crepidatella lingulata* (Gould, 1846)**

(Figures 1B, 7C)

Crepidula lingulata Gould, 1846: 160; 1852: pl. 32, fig. 481. Holotype USNM 5871. Puget Sound, Washington.

Crepidula bilobata “Gray,” Reeve, 1859: pl. 5, fig. 29. Four syntypes NHMUK 1977139. No locality given by Reeve (1859). California in NHMUK database.

Crepidula orbiculata Dall, 1919: 351. Holotype USNM 31100. Victoria, British Columbia, 60 fms.

Description. Shell to 25 mm, round to broadly oval, inflated, curved near apex, sometimes irregular outline; shell color white sometimes with brown or pinkish-brown markings; surface smooth, often covered with an orange-pink bryozoan (Fig. 7); apex, near posterior margin; septum convex, attached to shell along left side, posterior; development planktotrophic. Mantle often with either narrow or thick but tapering stripes ranging from cream to yellow (Fig. 1).

Distribution. Bering Sea, Alaska, to Mazatlan. Intertidal to 100 m. Common.

Remarks. *Crepidatella lingulata* shells are usually pale with thin or no periostracum. *Crepidatella orbiculata* appears to be an individual of *C. lingulata* with particularly heavy, grey-brown periostracum. However, some individuals of the very rare *C. charybdis* from northern California vary in the degree of sculpture (CAS 086096) and may be smooth and appear similar to *C. orbiculata*. In lot CAS 086096, the smooth shells look very similar to the types of *C. orbiculata*, while the sculptured ones are similar to the types of *C. charybdis*. The scarcity of shells and complete lack of preserved soft parts makes it impossible to determine the status of *C. orbiculata* with any certainty.

***Crucibulum* Schumacher, 1817**
(Figure 8B)

Crucibulum Schumacher, 1817: 182. Type species *Crucibulum planum* Schumacher, 1817 (SD Keen 1958: 247). Caribbean and Gulf of Mexico.

Dispotaea Say, 1824: 131. *Calyptraea costata* Say, 1820 (SD Olsson & Harbison 1953). Miocene, Maryland.

Description. Shell to 50 mm, conical; septum cup-shaped, attached at base, usually along left or posterior-left side.

Remarks. Primarily a tropical and South American group, one species occurs in the northeast Pacific.



FIGURE 8. *Grandicrepidula* and *Crucibulum*. A. *Grandicrepidula grandis* (Middendorff, 1849). LACM 1984-98.1, 55 m. Bering Sea, SW of Cape Newenham, Dillingham County, Alaska. Length 39 mm. B. *Crucibulum spinosum* (Sowerby I, 1824). LACM 17497, Anaheim Landing, Anaheim Bay, Orange County, California. Length 27 mm.

***Crucibulum spinosum* (Sowerby I, 1824)**

(Figure 8B)

Calyptraea spinosa Sowerby I, 1824 : no. 23, figs. 4, 7. More than one species figured and all figured material is lost.

Description. Shell to 35 mm, moderately elevated, with nearly circular base; apex twisted; sculpture radial rows of tubular spines, occasionally smooth on all or part of the shell; septum attached on left side from apex to edge of cup; color brownish, tan or white with darker rays in radial pattern.

Distribution. San Pedro, Los Angeles County, California, to Central America. Low intertidal to 90 m, on clam shells, rubble in shallow bays. Abundant.

Remarks. The name *Crucibulum spinosum* is currently applied to all of the Eastern Pacific *Crucibulum* with spines. This likely lumps several species with different development from the tropical east Pacific, as appears to be the case in the figure associated with the species description. However insufficient data are available at this time to properly revise this species group. Regardless of the name applied, only one species occurs in the northeast Pacific region covered by this work.

***Grandicrepidula* McLean, 1995**

(Figure 8A)

Grandicrepidula McLean, 1995: 80. Type species *Grandicrepidula grandis* Middendorff, 1849 (OD). Bering Sea.

Description. Shell to 60 mm; smooth, humped; aperture oval; apex posterior; septum broad, attached on both sides but further forward on right edge; one large muscle scar on left; mantle cavity to distal end of visceral mass; style sack, stomach ventral to mantle cavity.

Remarks. Only a single species occurs in northeast Pacific.

***Grandicrepidula grandis* (Middendorff, 1849)**

(Figure 8A)

Crepidula grandis Middendorff, 1849: 429–431, pl. 11, figs 8–10. Two Syntypes ZIN 11263/2 (Kantor & Sysoev 2006: pl. 23F). St. Paul Island, Bering Sea.

Description. Shell to 60 mm, large, robust, arched, white internally; apex excavated; shelf diagonal, slightly bowed, attached far forward on left; muscle scar distinct, rectangular, anterior to left corner of shelf; periostracum thick tan or brown; development unknown; osphradium even, tightly packed, bipectinate.

Distribution. Hokkaido, Japan, to Gulf of Alaska and north to at least Wade Hampton County, Alaska. Subtidal to 100 m. Uncommon.

Acknowledgements

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